Vision Research 89 (2013) 18–23

Contents lists available at SciVerse ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Luminance and contrast in visual perception of time to collision

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ARTICLE INFO

Article history:
Received 10 October 2012
Received in revised form 18 April 2013
Available online 11 July 2013

Keywords:
Luminance
Contrast
Looming
Time-to-collision
Evolution
Animal behavior

ABSTRACT

Many animals avoid dark, approaching objects seen against a lighter background but show no or weaker reactions to stimuli with inverted contrast. We investigated whether human observers would respond differently to such stimuli in terms of estimated time-to-arrival. We varied luminances of an approaching, light or dark disk and a plain, grey background, and for several conditions, continuously adjusted calibrations so as to keep contrast and/or overall lightness constant. Since no effects were found, we conclude that humans are able to discard luminance and contrast for the task at hand. Generally, however, performance was affected by different, consecutive regimes of feedback: Initially, without feedback, observers responded inconsistently and much too late; they improved after correct feedback, and in a third block of trials with pseudo-random feedback, they responded increasingly early without reverting to the initial level of uncertainty. We discuss our findings with regard to implications for neural mechanisms, put them in the context of evolutionary considerations, and propose continuative animal behavioral studies.

1. Introduction

In vision, *looming* refers to geometrical–optical, trigonometric magnification of a surface or surface patch during approach (Gibson, 1958). Avoidance responses to such stimuli have been observed in many animal species including humans of all ages (Ball & Tronick, 1971; Bower, Broughton, & Moore, 1970; Carlile, Peters, & Evans, 2006; Dunkeld & Bower, 1980; Hayes & Saiff, 1967; King et al., 1992; Schiff, Caviness, & Gibson, 1962; Tammero & Dickinson, 2002; Yamawaki, 2011). While some animals seem to respond at certain threshold values of the increasing visual angle (Robertson & Johnson, 1993; Schiff, 1965; Yamamoto, Nakata, & Nakagawa, 2003), others appear able to take approach velocity into account and compute time-to-collision (t_C) (Sun, Carey, & Goodale, 1992; Wang & Frost, 1992). Neural mechanisms mediating these responses have been described in some detail for several species, including crab (Oliva, Medan, & Tomsic, 2007), locust (Gabbiani et al., 2002; Gray, Blincow, & Robertson, 2010; Hatsopoulos, Gabbiani, & Laurent, 1995; Jones & Gabbiani, 2010; Rind, 1996, 1997; Rind & Simmons, 1992, 1999), goldfish (Preuss et al., 2006), frog (Ishikane et al., 2005), and pigeon (Frost & Sun, 1997, 2004; Sun & Frost, 1998; Wu et al., 2005; Xiao & Frost, 2009; Xiao, Li, & Wang, 2006). Importantly, some of these studies not only demonstrate looming or t_C sensitivity in the visual system but also a tight correlation (Wang & Frost, 1992) or even causal nexus (Preuss et al., 2006) with subsequent motor behavior. Less information is available for mammals, especially humans (Billington et al., 2010; Field & Wann, 2005; Graziano & Cooke, 2006; Liu, Wang, & Li, 2011; van der Weel & van der Meer, 2009).

Many animals respond only to a dark looming object seen against a lighter background, for example, crabs (*Uca pugnax*), frogs (*Rana pipiens*), and domestic Kimber chicks (Schiff, 1965), while others show weaker responses to contrast-inverted stimuli, for example, another species of crab (*Chasmagnathus granulatus*) (Oliva, Medan, & Tomsic, 2007) and locusts (Rind & Simmons, 1992). Again, matters are less clear for mammals. Recently, Münch et al. (2009) discovered approach-sensitive retinal ganglion cells in transgenic mice. These cells could be classified as OFF-type, that is, they were excited by light decrements and inhibited by light increments (Schiller, 1992, 1995; Westheimer, 2007). The cells responded to overall dimming, and also to rapid, 1.5–11.5 deg s^{-1} magnification of a dark bar, even during concomitant overall brightening of the visual field (with total light intensity remaining constant). The effective stimulus then, besides dimming, was near-symmetric expansion of a negative-contrast boundary. Münch et al. (2009) have not yet found corresponding ON-type cells (i.e., cells that are excited by light increments and inhibited by light decrements). Although the mouse may not always be the most appropriate model organism for humans (Huberman & Niell, 2011; Hughes, 1977; Van Hooser & Nelson, 2006; Vaughan et al., 2006), the similarities observed in the anatomy and functioning of eyes across different species or even taxa make derivation of hypotheses about vision mechanisms in humans, based on what is seen in other animals, not altogether unreasonable (Franz, 1934; Joselevitch & Kamermans, 2009; Lamb, Arendt, & Collin, 2009; Schiviz et al., 2008; Walls, 1942).

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0042-6989/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.visres.2013.06.009

We conducted two psychophysical experiments to test the conjecture that responses to looming by humans – like in most animals studied so far – are mainly driven by OFF-mechanisms (dark objects seen against a light background, or general light decrement) rather than ON-mechanisms (light objects seen against a dark background, or general light increment). Some previous work might suggest otherwise. Regan and Beverley (1978), acting as their own subjects, observed specific threshold elevations after adapting to a small, 0.5 deg visual angle, sinusoidally oscillating square, independently of sign of lightness contrast. Regan and Beverley's stimulus, however, may not compare well with looming that fills one's visual field, as conceived by Gibson (1958). Indeed, Beverley and Regan's (1979) finding that postadaptation thresholds remained unaffected by rectangles wider than 1.5 deg suggests that a different mechanism was tapped than the one responsible for the observed avoidance responses mentioned earlier (Simpson, 1988). On the other hand, Rind and Simmons (1992) and Oliva, Medan, and Tomsic's (2007) findings of weak responses to ON-stimuli in locust and crab may not generalize to mammals – humans in particular.

For our experiments we modeled achromatic looming stimuli after those of Münch et al. (2009). We expected negative-contrast stimuli to yield more precise t_C judgments than positive-contrast stimuli, irrespective of amount of contrast and overall lightness. In our general discussion, we will put our work in the context of evolution theory and ethological research.

2. Materials and methods

2.1. Participants

Two independent samples of 12 and 15 psychology undergraduates, respectively, participated in two experiments in partial fulfillment of a course requirement. In Experiment 1 there were 5 males and 7 females aged 22–36 years ($M = 25.9$, $SD = 4.25$), in Experiment 2 there were 6 males and 9 females aged 19 to 53 years ($M = 25.8$, $SD = 8.82$). Visual acuity and contrast sensitivity of observers were tested with a modified Landoldt display.

2.2. Stimuli and responses

Stimuli simulated head-on approach of an achromatic circular disk seen against a grey background. Screen size was 68 deg horizontal × 43 deg vertical visual angle. A chinrest stabilized head position. Viewing was "biocular" in the sense of Regan and Beverley (1978), that is, observers looked with both eyes but the simulation did not provide stereoscopic information. The disk was stationary for 2 s, then moved for 1–3 s at a fixed, constant speed of 4 m s^{-1}, and eventually vanished 1.5, 2, or 2.5 s prior to virtual collision. Observers were requested to press a button when they thought collision would have occurred (Carel, 1961; Schiff, 1986).

In order to prevent stereotyped responding, disk size and traveling distance were varied, yielding optical magnification of the disk from a minimum plane visual angle of 0.37–0.8 deg up to a maximum of 4–6.7 deg, with intermediate ranges in between. The first set of values closely matched those used by Regan and Beverley (1978) and Beverley and Regan (1979), the second one approximated those used by Münch et al. (2009).

2.3. Design and procedure

In order to reduce intraindividual variability and to test for effects of learning, experimental trials were initially blocked according to 3 different regimes of feedback. To obtain a baseline of performance, subjects received no feedback during the first block of trials. Proper feedback was provided during the second block. A short green bar was shown, and the word "perfect" popped up, when responses were correct within a tolerance of ±250 ms of the true time of the disk's arrival. The bar was extended to the left for early responses (-250 ms > t_R > -500 ms) and to the right for late ones (+250 ms < t_R < +500 ms). In both cases, the bar's color turned red, and the words "too early" or "too late", respectively, appeared. For responses more than ±500 ms off the mark, the bar's color turned purple, and the words "much too early" or "much too late" appeared. During the third block of trials, feedback was pseudo-randomly assigned with the feedback "perfect" having a 60% probability to appear, and the other four possible feedbacks a 10% probability each. The purpose of this improper feedback was to test for the robustness of the reinforced responses from the second block of trials.

Experiments comprised four stimulus variants (details to be described below), two disk sizes, three presentation times, three extrapolation times, and three conditions of feedback, altogether making for 216 trials, each of which was repeated twice. Order of trials was random within the four blocks of stimulus types. Those blocks were presented in a randomized order within the three blocks of feedback conditions. Twelve practice trials with our four kinds of stimuli, but partly different parameters, were run before each experiment. Two short breaks were taken after one and two thirds of experimental trials (i.e., between the different feedback blocks). A complete session, comprising tests, practice, and experiment, lasted about 45–60 min.

3. Experiment 1

3.1. Stimuli

There are several possibilities to construct looming stimuli of constant contrast and constant overall lightness. In Table 1, we list those that we used. For Experiment 1, we only varied lightness of the looming object. In one condition, a black or white disk during motion gradually assimilated to the grey background, keeping overall lightness constant. This stimulus corresponds to a real-world scenario across the course of which an approaching object or animal (say, a predator) undergoes a change of surface reflectance, as might happen through local increases of illumination or cast shadows. Optically, this is a complex stimulus because, along with the brightening or darkening of the object there is a change (in our case, a reduction) of contrast between object and background. In a second condition, black and white disks of constant lightness were used. These stimuli, while keeping contrast constant, imply a decrease or increase of overall lightness, respectively.

3.2. Results

Data were analyzed in terms of signed errors (time of subjects' responding [t_R] minus objective t_C). As is evident from the plots in

Table 1
Overview of stimuli used in Experiments 1 (upper panel) and 2 (lower panel).

Object	Background	Contrast	Overall lightness
Black	Grey	Constant	Darkening
White	Grey	Constant	Brightening
Black, brightening	Grey	Decreasing	Constant
White, darkening	Grey	Decreasing	Constant
Black	Grey, brightening	Increasing	Constant
White	Grey, darkening	Increasing	Constant
Black, brightening	Grey, brightening	Constant	Constant
White, darkening	Grey, darkening	Constant	Constant

Note. Constant overall lightness was 21 cd m^{-2}.

Fig. 1, observers initially responded about half a second too late. A Greenhouse–Geisser corrected analysis of variance (ANOVA) with the repeated-measures factors *stimulus* and *feedback* revealed no effects of our variations of luminance and contrast and no interaction between stimulus type and feedback condition. Our feedback regime proved very effective: Participants responded significantly earlier, $F(1,11)_{M,\ 1\ vs.\ 2} = 9.994$, $p = .009$, $\eta_P^2 = .476$, and also more consistently, $F(1,11)_{SD,\ 1\ vs.\ 2} = 19.404$, $p = .001$, $\eta_P^2 = .638$, during the second block of trials as compared to the first one (Fig. 2). Subjects intensified the shift to early responding when provided with random feedback during the third feedback block, thereby increasing the absolute value of their average error again, $F(1,11)_{M,\ 2\ vs.\ 3} = 9.622$, $p = .010$, $\eta_P^2 = .467$; however, participants did not revert to the level of uncertainty that they displayed in the first block, $F(1,11)_{SD,\ 2\ vs.\ 3} = 1.928$, $p = .192$, $\eta_P^2 = .149$. A comparison of response behavior during first and third feedback blocks also yielded significant differences, $F(1,11)_{M,\ 1\ vs.\ 3} = 11.344$, $p = .006$, $\eta_P^2 = .508$; $F(1,11)_{SD,\ 1\ vs.\ 3} = 16.293$, $p = .002$, $\eta_P^2 = .597$ (all F ratios refer to simple contrasts).

In an additional repeated-measures ANOVA we examined the effects of those experimental variables that were not the focus of our present research but had been included to discourage participants from using simple heuristics when judging t_C. Effects were as usual: Larger disk size (DeLucia, 1991) and longer extrapolation times (Schiff & Detwiler, 1979) yielded earlier responses, $F(1,11)_{Size} = 51.105$, $p < .001$, $\eta_P^2 = .823$; $F(1.804,19.849)_{Extrapolation} = 38.654$, $p < .001$, $\eta_P^2 = .778$. There were also several simple and higher-order interactions which we do not report in detail because they are not relevant regarding the question of this study.

3.3. Discussion

Results support Regan and Beverley's (1978) contention that visual perception of looming in humans is invariant across direction of lightness contrast. While Regan and Beverley showed this for very small oscillating stimuli in an adaptation paradigm, we demonstrate the same for both small and larger, continuously magnifying stimuli in an extrapolation paradigm. Additionally, we show that a decrease in contrast as well as an overall decrease or increase of lightness do not interfere. Stimulus variants of Experiment 1 did not yet exhaust all possible combinations of changes or constancy of lightness and contrast between object and background. Therefore, in Experiment 2, we explored the missing cases.

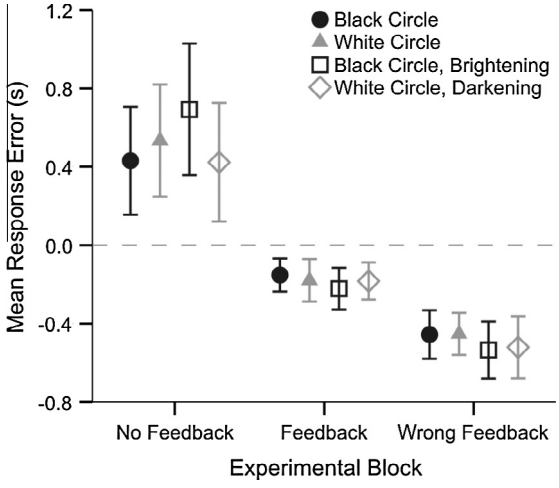

Fig. 1. Errors of estimated time-to-collision (t_C), calculated as estimated t_C minus actual t_C, for the four stimuli under the three feedback conditions of Experiment 1. Error bars represent standard errors of the mean of 12 participants.

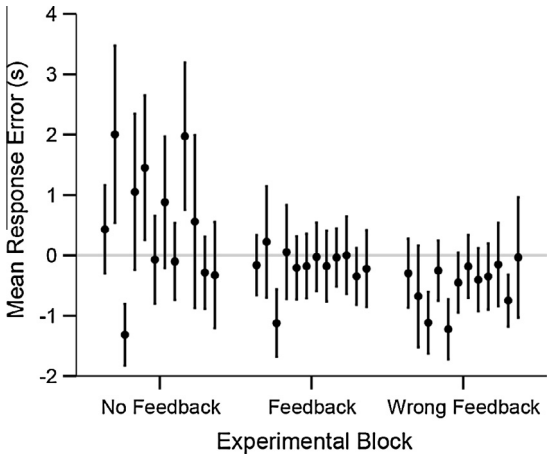

Fig. 2. Constant and variable errors of estimated time-to-collision (t_C, calculated as estimated t_C minus actual t_C) for each participant under the three feedback conditions of Experiment 1. Response errors were averaged across all trials and all four stimuli. The same order of participants is shown in each feedback condition. Error bars represent standard deviations across all response errors of each participant.

4. Experiment 2

4.1. Stimuli

For Experiment 2, we varied both the lightness of the looming object and that of the background (Table 1). Again, at the start of a trial, a black or white disk appeared in front of a grey background. In one condition, during motion, the black disk brightened, and the white disk darkened. Concomitantly, the background brightened or darkened too so as to maintain a constant level of overall lightness, and also constant contrast between object and background (Münch et al., 2009). These stimuli correspond to real-world scenarios across the course of which there occur global and local changes of illumination (e.g., through broken clouds and – again – cast shadows). In a second condition, we used a black and a white disk seen in front of a continuously brightening or darkening grey background. These stimuli also keep overall lightness constant but yield increasing contrast.

4.2. Results and discussion

Again, no effects of contrast or lightness were seen (Fig. 3). Thus, Experiment 2 further corroborates the hypothesis that human responses to impending collisions are unaffected by changes in lightness and contrast. Effects of feedback (Fig. 4) and the other experimental variables were similar to the ones observed in Experiment 1. Comparing the three feedback conditions, we obtained: $F(1,14)_{M,\ 1\ vs.\ 2} = 12.157$, $p = .004$, $\eta_P^2 = .465$; $F(1,14)_{SD,\ 1\ vs.\ 2} = 12.157$, $p < .004$, $\eta_P^2 = .465$; $F(1,14)_{M,\ 2\ vs.\ 3} = 7.569$, $p = .016$, $\eta_P^2 = .351$; $F(1,14)_{SD,\ 2\ vs.\ 3} = 1.850$, $p = .195$, $\eta_P^2 = .117$; $F(1,14)_{M,\ 1\ vs.\ 3} = 15.687$, $p = .001$, $\eta_P^2 = .528$; $F(1,14)_{SD,\ 1\ vs.\ 3} = 23.062$, $p = .001$, $\eta_P^2 = .622$ (again, all F ratios refer to simple contrasts). Hence, the general trends observed in Experiment 1 were met again: Correct, and subsequently applied pseudo-random feedback induced increasingly earlier responding, which also was more consistent than during the first, baseline block.

5. General discussion

Compared to the precision of pigeons' responses to impending collisions (Wang & Frost, 1992), the performance of most other animals mentioned in Section 1 is much less precise and sophisticated.

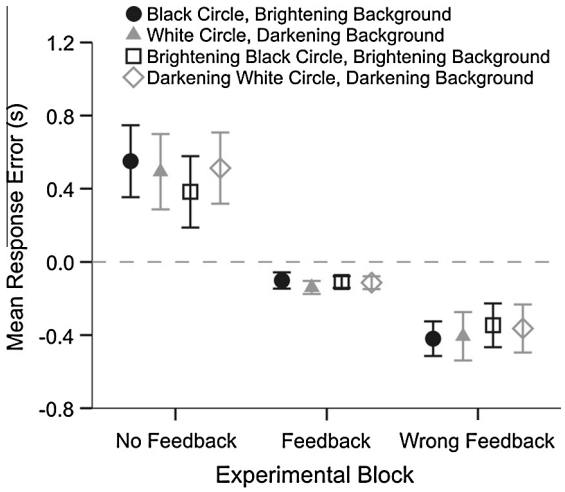

Fig. 3. Errors of estimated time-to-collision of Experiment 2, calculated as for Experiment 1 (estimated t_C minus actual t_C). Error bars represent standard errors of the mean of 15 participants.

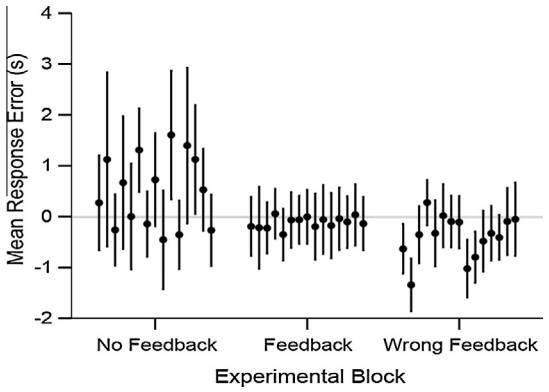

Fig. 4. Constant and variable errors of estimated time-to-collision (t_C, calculated as estimated t_C minus actual t_C) for each participant under the three feedback conditions of Experiment 2. Response errors were averaged across all trials and all four stimuli. The same order of participants is shown in each feedback condition. Error bars represent standard deviations across all response errors of each participant.

The performance level of humans at this task is more difficult to evaluate because of ethical constraints regarding research settings and methods (but cf. King et al., 1992; Li & Laurent, 2001, for the use of immediate behavioral measures). However, according to our present findings, humans appear more flexible than many other animals in being able to discard luminance and direction of contrast in the stimulus.

Generally, whether or not a species will be endowed with temporal abilities depends on its ecological niche (Frost, 2010). For *aves* – prey or predator – timely responses are obviously advantageous, guaranteeing safe evasion or successful hits during flight at minimum energy expenditure. The evolution of *homo* is less easily traced (Klein, 2008). With humans, both predatory behavior as well as the avoidance of falling prey to others require social action. Still, for each individual, temporal precision in manipulative or locomotor activities may be an advantage, although this may only hold for a certain level of precision. The long known but only recently emphasized fact of great interindividual variability in human t_C behavior (Landwehr et al., 2010; Simpson, 1988) can be interpreted to mirror the uncertain status of temporal demands in the hominid evolution.

However, humans may compensate for deficits by means of training, as exemplified by impressive achievements in sports (Bootsma & van Wieringen, 1990; Regan, 2012). The effects of feedback we found in our present work also testify to the malleability of human performance in a t_C task. From a descriptive-behaviorist point of view (Skinner, 1953), feedback about the correctness of a response may work like positive reinforcement, and feedback about an error (or failure) may act as a negative reinforcer. In order to understand the effects of our quasi-random feedback, a cognitive interpretation seems to be required (cf. Spielberger, Bernstein, & Ratliff, 1966; Tolman, 1932) as subjects will probably note the frequent mismatch between their behavior and the consequence provided by the experimenter. If so, they have to consider ways to deal with this mismatch. Indeed, many of our participants noticed that there was something odd about the feedback schedule in the final block of trials, and some even complained that ours had been a "mean experiment"! Anyhow, there were remarkable interindividual differences in observers' susceptibility to feedback. For example, inspection of Fig. 2 reveals that subject No. 2 responded increasingly early across feedback blocks whereas subject No. 3 responded early throughout, and thus seems to have been unaffected by feedback conditions. The causes of these differences between individuals remain elusive for now (Landwehr et al., 2010). Correct feedback, however, enabled the majority of our participants to improve their performance considerably.

The research question from which we had started out our present work had been whether or not the sign of lightness contrast would matter for t_C responses. The answer, for humans, seems to be *no*. With regard to mechanisms, this implies that either, in addition to the kind of OFF-mechanism found by Münch et al. (2009) in mice, another retinal mechanism responsible for ON-stimuli must be present in man, or some later mechanism must balance any early bias, or responses to looming are not generated in the retina at all but further downstream. Indeed, functional-magnetic-resonance-imaging (fMRI) studies show that in man, impending-collision stimuli and judgmental t_C responses – both in a prediction-motion paradigm as we used it, as well as in a relative-judgment task – activate specific cortical areas (Billington et al., 2010; Field & Wann, 2005; cf. Lugtigheid & Welchman, 2011; Tresilian, 1995, for a comparison of paradigms). Hence, it is quite conceivable that the retinal, approach-sensitive mechanism which Münch et al. (2009) discovered in mice, is a specific adaptation in this species that evolved under the predatory selection pressure to which it is exposed.

Although Münch et al. (2009) provide some suggestions about how the output of the retinal ganglion cells they studied might feed into more sophisticated neural mechanisms that eventually may allow for the computation of t_C, they did not investigate these matters any further. In all amniots there are two major pathways from retina to cortex along which approach- and looming-related signals might travel, the geniculo-striate (or thalamofugal) and the colliculo-extrastriate (or tectofugal) pathways (Shimizu & Bowers, 1999). For birds (pigeons at least) it is known that t_C sensitivity is confined to the tectofugal path (Wang & Frost, 1992; Wu et al., 2005; Xiao, Li, & Wang, 2006). It is generally agreed that the mammalian homolog of that path is the collicular pathway (Guirado, Real, & Davila, 2005). Although this pathway has been implicated to be responsible for quick responses to novel and/or threatening stimuli (Dean, Redgrave, & Westby, 1989; DesJardin et al., 2013), there is scant evidence that it deals with looming stimuli (Liu, Wang, & Li, 2011; Schneider, Carman, & Ayres, 1987). On the other hand, Kay et al. (2011; cf. Rivlin-Etzion et al., 2011) found, again with transgenic mice, that direction-of-motion sensitive retinal ganglion cells project to both the lateral geniculate nucleus and to the superior colliculus, leaving open the possibility of parallel processing of information at least in mammals.

It is an intriguing question for evolution theory why the two retino-cortical pathways differentiated differently in the sauropsid and mammalian lineages that emanated from a common ancestral amniote stock. At the behavioral level the challenge is to develop a paradigm that renders t_C-critical performance comparable between the taxa (classes). In a candidate set-up, developed by Ilany and Eilam (2008; also cf. Fux & Eilam, 2009), barn owls and spiny mice were observed regarding their respective tactics of attack and escape. The mice *either* fled late at high speeds *or* early (i.e., when the predator was still at a great distance). The owls' attacks were triggered by the prey's initiation or cessation of locomotion. These studies focused on flight initiation distance instead of t_C, but could be adapted. For an exhaustive comparison, both avian and mammalian predators have to be found that feed on both kinds of prey. Obviously, for a fair comparison of animals and humans, something different is needed.

With regard to the approach-sensitive retinal mechanism detected by Münch et al. (2009), supplementary behavioral experiments may also be informative. The mechanism was studied under photopic conditions and found to serve a completely different function in the dark – with the information flow being reversed so as to amplify rod signals. Several species of mice are diurnal, others nocturnal, and others display a dual life style (Chalupa & Williams, 2008). Only experiments with freely roaming animals (cf. Oliva, Medan, & Tomsic, 2007) or well-controlled field studies can show how effective a mechanism is in a given species under these different conditions of illuminance. Similarly, it may be revealing to test our stimuli with a different response measure other than mere button presses.

In this context, some limitations of our present research have to be acknowledged. For our experiments, we sampled only one level of luminance and few levels of contrast. It will be of interest to see whether our results replicate across a broader range of luminances (including scotopic conditions) and contrasts. Also, it would be interesting to see whether they generalize to complex scenes.

Contributors

K.L., E.B., and H.H. designed experiments, E.B. supervised data collection and analyzed data. K.L. wrote the manuscript, integrating comments from E.B. and H.H. All authors have approved the final article.

Acknowledgments

The work presented in this paper was supported by a grant of the Deutsche Forschungsgemeinschaft [HE 2122/6-2 to H.H.].

We thank Günter Meinhardt for loan of photometric apparatus, and Miriam Hemmersbach and Stephanie Preuß for collecting data.

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